DISTANCE-DEPENDENT SURVIVAL AND DISTRIBUTION OF JUVENILE CORALS: JANZEN-CONNELL EFFECTS DO NOT OPERATE ON TWO BROODING INDO-PACIFIC CORALS

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David A. Gibbs

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DISTANCE-DEPENDENT SURVIVAL AND DISTRIBUTION OF JUVENILE CORALS: JANZEN-CONNELL EFFECTS DO NOT OPERATE ON TWO BROODING INDO-PACIFIC CORALS

Approved by:

Dr. Mark Hay, Advisor
School of Biology
Georgia Institute of Technology

Dr. Marc Weissburg
School of Biology
Georgia Institute of Technology

Dr. Daniel Gleason
Department of Biology
Georgia Southern University

Dr. Joshua Weitz
School of Biology
Georgia Institute of Technology

Dr. Lin Jiang
School of Biology
Georgia Institute of Technology

Date approved: April 22, 2014

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CSR- Complete spatial randomness

GLM- Generalized linear model

MPA- Marine protected area

SUMMARY

The Janzen-Connell hypothesis proposes that species-specific enemies promote species coexistence through distance- and density-dependent survival of offspring near conspecific adults. I tested this hypothesis experimentally by transplanting juvenile-sized fragments of two species of brooding corals varying distances from conspecific adults, and observationally by assessing the spatial distribution of those two species in the field. Small fragments (as proxies for ≈6 month old juveniles) of *Pocillopora damicornis* and *Seriatopora hystrix* were transplanted 3, 12, 24 and 182 cm upstream and downstream (relative to the prevailing current) of conspecific adults and their survivorship and condition (bitten off, overgrown by algae, or bleached) checked every 1-2 d. I also characterized the spatial distribution of *P. damicornis* and *S. hystrix* within replicated plots on three Fijian reef flats and measured densities of small colonies within 2 m of larger colonies of each species.

Contrary to the Janzen-Connell hypothesis, juvenile-sized transplants exhibited no differences in survivorship as a function of distance from adult *P. damicornis* or *S. hystrix* and *P. damicornis* and *S. hystrix* were aggregated rather than overdispersed on natural reefs. Survival unaffected by distance from focal colonies as well as certain recruitment processes could generate the observed aggregation. I did observe predation of *P. damicornis* that was spatially patchy and temporally persistent due to feeding by the territorial triggerfish *Balistapus undulatus*. This patchy predation did not occur for *S. hystrix*. Thus, I found no support for the Janzen-Connell hypothesis, but did document hot-spots of species-specific corallivory that could create variable selective regimes on an otherwise more uniform environment, and help maintain the high diversity of corals typical of Indo-Pacific reefs.

CHAPTER 1: INTRODUCTION

The coexistence of many seemingly similar species in tropical rainforests and coral reefs has long been a subject of investigation (Connell 1978). One suggested mechanism for the maintenance of diversity is the Janzen-Connell hypothesis (Janzen 1970; Connell 1971), which proposes that species-specific enemies clustered near adults increase the mortality of conspecific juveniles nearby and thus prevent any single species from monopolizing local resources. This hypothesis has generally been applied to long-lived, stationary, terrestrial organisms such as trees (Zhu et al. 2013). As a result of distance- and density-dependent mortality of offspring mediated by species-specific enemies, the Janzen-Connell hypothesis predicts that conspecifics' spacing will be overdispersed rather than random or clumped. Support for the hypothesis from studies of terrestrial plant communities has been mixed. Although there are a few examples of species-specific distance- or density-dependent mortality and their effects on community species richness (e.g. Clark and Clark 1984; Packer and Clay 2000; Bell et al. 2006; Petermann et al. 2008; Bagchi et al. 2014), meta-analysis has found no net effect of distance from parent on offspring mortality across a variety of plant types, habitats, or life stages (Hyatt et al. 2003). Thus, some tree species may experience Janzen-Connell effects (Johnson et al. 2012) but it appears that most do not (Hyatt et al. 2003).

The Janzen-Connell hypothesis has been tested almost exclusively in terrestrial plant communities despite also being relevant to benthic marine communities. This may partially be because the Janzen-Connell hypothesis assumes that dispersal decreases monotonically with distance from parents and that the average dispersal distance is greater than the average predation distance but on the same order of magnitude (Nathan and Casagrandi 2004), neither of which

necessarily applies to marine species with dispersive, pelagic larvae. More specifically, the Janzen-Connell hypothesis has not often been invoked as a mechanism for the maintenance of coral diversity, perhaps because corals do not so clearly have the equivalent of seed shadows or many species-specific enemies (Cornell and Karlson 2000). Instead, explanations for maintenance of coral diversity often invoke disturbance regimes, abiotic gradients (e.g. light, sedimentation), competition hierarchies, and differential mortality (Lang 1971; Connell 1978; Buss and Jackson 1979; Porter et al. 1981). Larvae of both brooding and broadcast spawning corals are competent to settle for days to months after release (Richmond 1987; Miller and Mundy 2003; Nozawa and Harrison 2008) and may disperse up to hundreds of kilometers (Jones et al. 2009; Torda et al. 2013). Therefore, unlike the passively transported seeds of many tree species, coral settlement need not be greatest closest to parents. Nevertheless, Janzen-Connell mechanisms could affect both brooding and broadcasting corals because their larvae can choose where to settle, which could lead to larvae settling near conspecific adults or in aggregations (e.g. Dunstan and Johnson 1998). Even if distant colonies contribute most of the recruits near some conspecifics, Janzen-Connell mechanisms could still operate on those aggregations. Two further reasons to expect Janzen-Connell mechanisms to affect brooding corals is that their planulae frequently settle quickly after release and thus close to their parents (Carlon and Olson 1993; Tioho et al. 2001; Torda et al. 2013) and that brooding corals may need to live in close proximity for broadcasted sperm to successfully fertilize eggs inside conspecific colonies (Brazeau and Lasker 1992, and see Grosberg 1987 for an example with a brooding, colonial ascidian).

While some corallivorous fish and mollusk species are specialists or at least have strong dietary or habitat preferences (Pratchett 2007; Cole et al. 2010; Schoepf et al. 2010; Pratchett et al. 2013), the scant research on the Janzen-Connell hypothesis's application to corals suggests

that microorganisms constitute the species-specific enemies concentrated near adults and may thus represent significant threats to nearby juveniles of the same species. Marhaver et al. (2013) used a series of lab and field experiments in the Caribbean to attribute higher mortality of *Orbicella* (formerly *Montastrea*) *faveolata* (Budd et al. 2012) recruits placed near adult conspecifics to bacterial enemies. However, they found a complex relationship between distance from adult colonies, current direction, and recruit mortality. In less direct tests of the Janzen-Connell hypothesis, Vermeij (2005) and Vermeij and Sandin (2008) observed that juvenile coral survival decreased as conspecific cover increased, which they hypothesized was due to species-specific microorganisms rather than to saturation of the limiting space resource.

I tested the distance-dependent mortality mechanism behind the Janzen-Connell hypothesis and examined the spatial pattern for conformity with Janzen-Connell predictions in two species of brooding corals on Fijian reef flats. Comparing the observed spatial pattern to that predicted by the Janzen-Connell hypothesis may indicate the relative strength of Janzen-Connell effects on the reef. This is the first test of the Janzen-Connell hypothesis among brooding corals, as well as the first test in the species-rich Indo-Pacific. I tested distance-dependent mortality by transplanting small fragments of *Seriatopora hystrix* and *Pocillopora damicornis* (as proxies for ≈6 month old juveniles) different distances from adult conspecifics and monitored their survival every 1-2 d for 1 or 2 months, respectively. I chose these two species because of their potentially short dispersal distances due to brooding, increasing the likelihood of observing Janzen-Connell effects. To evaluate whether Janzen-Connell forces might affect colony spacing on the reef over longer periods of time, I also surveyed the spatial distributions of *S. hystrix* and *P. damicornis* and their distances from adult conspecifics on three reef flats.

CHAPTER 2: METHODS

2.1 Study site characteristics

This study was conducted on reef flats within no-take marine protected areas (MPAs) adjacent to Votua, Vatuo-lailai, and Namada villages along the Coral Coast of Viti Levu, Fiji. These reserves are scattered along an 11 km stretch of fringing reef and are separated by ≈3-8 km. The reserves are characterized by high coral cover (≈38-56%), low macroalgal cover (≈1-3%), and a high biomass and diversity of herbivorous fishes (Rasher et al. 2013, Bonaldo and Hay 2014). The reef flats range from ≈1-3 m deep at high tide, extend ≈500-600 m from shore to the reef crest, and are typical of exposed reef flats occurring throughout Fiji. Except during low tides in calm weather, waves push waters over the reef front and waters flow directionally across the reef flats to discharge through deeper channels separating sections of the flat. This creates a relatively predictable current direction at most locations on the flat. Out-plants of juvenile coral fragments were conducted between August and October 2013 and in Votua village's MPA only. Surveys of coral sizes and distribution were conducted in all three villages' MPAs during the same months.

2.2 Survival experiments

To test whether juvenile corals experienced distance-dependent mortality near adult conspecifics, I collected small fragments of *P. damicornis* and *S. hystrix* (as proxies for ≈6 month old juveniles [Sato 1984]), selected suitable adult focal colonies (defined below), and attached the fragments 3, 12, 24 and 182 cm up- and down-current from each focal adult. These distances were used for ease of comparison with prior research (Marhaver et al. 2013). I

deployed fragments roughly east and west of focal colonies (up- and down-current of water flow) in Votua's MPA.

I collected 16 fragments of 30-40 polyps each from the tops of 24 large *P. damicornis* colonies of similar morphology from the Votua village MPA. This was achieved by collecting 16 fragments from each of four source colonies in six rounds over two days. Each collection was taken to shore and four fragments (one from each source colony) were epoxied (Emerkit epoxy) onto the unglazed side of 16 2.54 x 2.54 cm tiles. Thus, each tile had fragments from four different colonies and sets of 16 tiles had fragments from the same four colonies. After epoxying, tiles were held in a shaded tub of seawater for ≈1 h, allowing the epoxy to harden. Tiles were then cable-tied onto metal racks at ≈1 m deep in the MPA. These fragments acclimated for two weeks before being used in the experiment. Survivorship during acclimation was 100%, producing 384 fragments on 96 tiles.

Within the MPA, 10 adult *P. damicornis* colonies served as focal colonies. Focal colonies: i) were >10 cm at their smallest diameter (range was 10 to 35 cm for *P. damicornis* and 10 to 75 cm for *S. hystrix*), ii) had no other *P. damicornis* colonies within 4 m (so as not to confound effects of the focal colony with effects of nearby conspecifics), and iii) had clear space for 190 cm PVC pipes to be placed roughly east and west without disturbing other corals. I recorded each focal colony's approximate depth at high tide, resident fish (if any), and size (taking photos from above and tracing colonies' perimeters using ImageJ [Rasband 1997]).

PVC pipes served as platforms to which I attached the tiles. Each pipe was 20 mm across and 190 cm long. Pipes were anchored to the reef by driving steel rebar through pre-drilled holes and cementing the rebar to the pipe. Notches of 2.54 cm allowed me to cable-tie tiles (holding

coral fragments) onto the pipes at distances of 3, 12, 24 and 182 cm from focal colonies. This approach successfully secured all pipes and tiles throughout the experiment.

Each tile was randomly assigned to a position (distance and direction) on one of the 20 pipes; unassigned tiles were kept on the rack as spares (64 fragments on 16 tiles). Thus, fragments at each distance and around each focal colony were random with respect to source colony.

Every 1-2 d after tile deployment, I examined the fragments around the focal colonies and those on the spare tiles on the rack, recording survivorship, partial or full disappearances, overgrowth by algae, bleaching, or other changes in status.

On some tiles, three or four of the four fragments disappeared within a 24 h period between checks on their condition, appearing to have been bitten off. To determine the causes of this localized mortality, I replaced tiles whose four fragments had been eaten with spare tiles holding four healthy fragments around three of the focal colonies that had experienced localized mortality and videotaped them (GoPro II HD with BatteryPac) from about 1 m away during the following high tides. Cameras were retrieved after battery exhaustion (about 2 h) and the videos watched.

Seriatopora hystrix was treated identically except that there were no episodes of localized mortality for this species, and thus no need to deploy spare tiles. As with *P. damicornis*, fragments on the spare tiles neither bleached nor died during the experiment (64 fragments on 16 tiles).

I evaluated survival patterns using mixed-effects Cox proportional hazards survival models (the coxme package, Therneau 2012) in R (R Core Team 2013). In the full model, distance and direction from focal colony were fixed effects and focal colony and tile nested

within focal colony were random effects because fragments were blocked by tile and focal colony. The size of the focal colony and the depth of the tiles were also included as random effects.

2.3 Distribution surveys

I characterized the spatial distribution of *P. damicornis* and *S. hystrix* in the reef flat MPAs of Namada, Vatuo-lailai, and Votua villages at two scales. For my larger-scale survey, I mapped each colony within 8 x 8 m plots (N=5, 5, and 10 for Namada, Vatuo-lailai, and Votua, respectively). Each plot was divided into 128 0.5 x 0.5 m cells and each coral mapped into a cell. The location of each survey plot was determined by randomly choosing a point on shore, swimming 100, 200, or 300 kicks directly away from shore at that point, and surveying the closest bommie large enough to fill more than three quarters of an 8 x 8 m plot. In four of 10 surveys at Votua and in all five surveys at Vatou-lailai and Namada, I also measured the largest diameter of each *P. damicornis* colony. I did not measure *S. hystrix* colony size because individual colonies were more frequently discontinuous. To avoid confounding biotically-driven spatial distribution with patterns caused by patchily distributed substrate types, I also recorded which cells were comprised primarily of unstable substrates such as sand-scoured pools or channels and bommie tops covered in dead coral rubble ("unsuitable habitats").

I analyzed these data using the neighborhood density function O(r) in the point pattern analysis program Programita (Wiegand and Moloney 2004). This analysis identifies distances at which individuals are aggregated, randomly spaced, or overdispersed compared to a specified null model. Unlike the more frequently used Ripley's K(r) statistic, each distance category is not affected by those inside it; expected aggregation at each distance is compared to the observed

value independently of nearer distances. Each concentric ring centered on an individual coral is separately placed on the aggregated-overdispersed continuum and displays the spatial pattern within a different distance category. Ring width was 0.5 m extending up to 4 m. The null model for this analysis was complete spatial randomness (CSR), which assumes that colonies have an equal likelihood of occurring anywhere in the plot. Because the variance in substrate types violated the assumption of uniform likelihood, I conducted the below analyses once using the entirety of all 8 x 8 m plots and a second time excluding cells of unsuitable habitat (which should better meet CSR's assumption of uniform likelihood).

To determine whether the observed spatial pattern was random or significantly aggregated or overdispersed, Programita simulated placement of each plot's colonies 999 times using CSR, calculating O(r) for each simulation, then combined replicate O(r)'s from each reef and from all three reefs. This generated a distribution of simulated O(r)'s from which I established the significance of the observed spatial patterns. The distance(s) at which significant aggregation or overdispersion occurred were determined by the distances at which the observed pattern fell above or below the 95% simulation envelopes, respectively.

In addition to analyzing all *P. damicornis* and *S. hystrix* colonies, I analyzed *P. damicornis* <5 cm, $\geq$5 cm, $\geq$10 cm, and $\geq$15 cm in diameter to see if spatial patterns changed with colony size. The <5 cm and $\geq$5 cm categories were mutually exclusive but because there were not enough colonies between 5 and 10 cm, 10 and 15 cm, and $\geq$15 cm to analyze as mutually exclusive groups, larger size categories were subsets of the smaller ones (e.g. all corals within the $\geq$15 cm group were included in the $\geq$10 cm group).

The 8 x 8 m quadrat surveys could not resolve spatial patterns below the cell size of 0.5 x 0.5 m, meaning that patterns occurring at less than 0.25^2 m would be undocumented. To

determine the spatial distribution of *P. damicornis* and *S. hystrix* at smaller scales, I conducted 2 m radius circular surveys around focal *P. damicornis* and *S. hystrix* colonies that met the following criteria: i) they were the largest colony of that species within 4 m (to reduce the effects of conspecifics), and ii) > 75% of the substrate within 2 m was suitable habitat for *P. damicornis* and *S. hystrix*, again to homogenize the likelihood of colonies occurring everywhere in the survey (as defined above for the quadrat surveys).

The distance to each surrounding (radial) *P. damicornis* and *S. hystrix* colony was the average of the distance to that colony's near and far sides (N=45 focal colonies for *P. damicornis* around *P. damicornis*, 10 for *S. hystrix* around *P. damicornis*, and 24 each for *P. damicornis* and *S. hystrix* around *S. hystrix*). I analyzed radial colony counts in 10 cm concentric rings using a generalized linear mixed effects model with Poisson errors and the canonical log link function implemented with the lme4 package in R (Bates et al. 2013). Distance was a fixed effect and focal colony with distance nested inside was a random effect, with the $\log_{10}$ of the ring sizes as an offset to control for unequal area sampled at each distance (i.e. ring area increased with distance from the focal colony). I repeated this analysis with just the closest 0.5 m and 1 m of the circles in case radial colonies beyond those distances were masking any short-range effects of the focal colonies.

I also analyzed the *P. damicornis* data from the 8 x 8 m plots in the same manner as the circular surveys. To convert the plot data, an R script identified every surveyed *P. damicornis* colony $\geq$2 m from all edges of its plot and equal to or larger than a specified diameter (either 15 or 20 cm) as a focal colony (N=38 and 19 focal colonies, respectively). Unlike with the circular surveys, I did not restrict focal colonies to those that were the largest within 4 m in order to have an appreciable sample size. The script then calculated the distances to all *P. damicornis* colonies

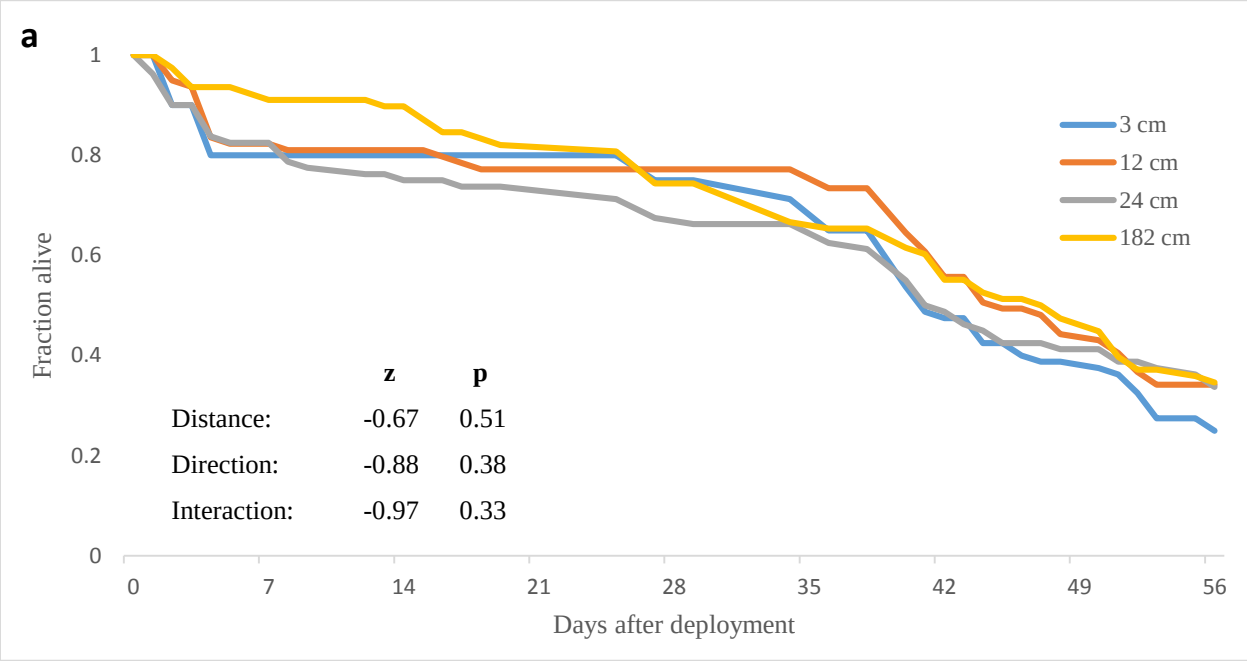
less than the specified diameter within 2 m and placed them into 10 cm concentric rings as above. I used generalized linear mixed effects models as described for the circular surveys.

CHAPTER 3: RESULTS

3.1 Survival experiments

In my field experiment, neither distance nor direction from focal colony significantly affected survival of *P. damicornis* or *S. hystrix* fragments (Figure 1). I observed three categories of fragment death: algal overgrowth without bleaching, bleaching preceding death in place (potentially due to microbes [e.g. Ben-Haim et al. 2003]), and partial or complete disappearance, putatively due to predation (akin to Penin et al. 2011). There were not enough cases of algal overgrowth to conduct survival analysis; this occurred to five *P. damicornis* fragments across three distances and one *S. hystrix* fragment. Bleaching (47 and 46 fragments out of 320 for *P. damicornis* and *S. hystrix*, respectively) of either species was not affected by distance or direction (Figure 2). Finally, distance and direction did not affect the number of *P. damicornis* fragments that partially or fully disappeared from the epoxy (putative predation), and direction did not affect this for *S. hystrix* but distance was significant ($z=2.23$, $p=0.03$) (Figure 3), with death from putative predation tending to increase with distance from the focal colony.

Approximately 15% of the *P. damicornis* and *S. hystrix* fragments I transplanted around focal colonies bleached, while 0% of the 64 fragments of each species on the coral rack bleached despite being at a similar depth on the same reef (Cox proportional hazards survival analysis, likelihood ratio for *P. damicornis*=16.5, likelihood ratio for *S. hystrix*=24.7, $p<0.0001$ for both species). However, fragments on the coral rack were ≈1 m above the benthos, while fragments deployed on PVC pipes were 5-15 cm above the benthos.



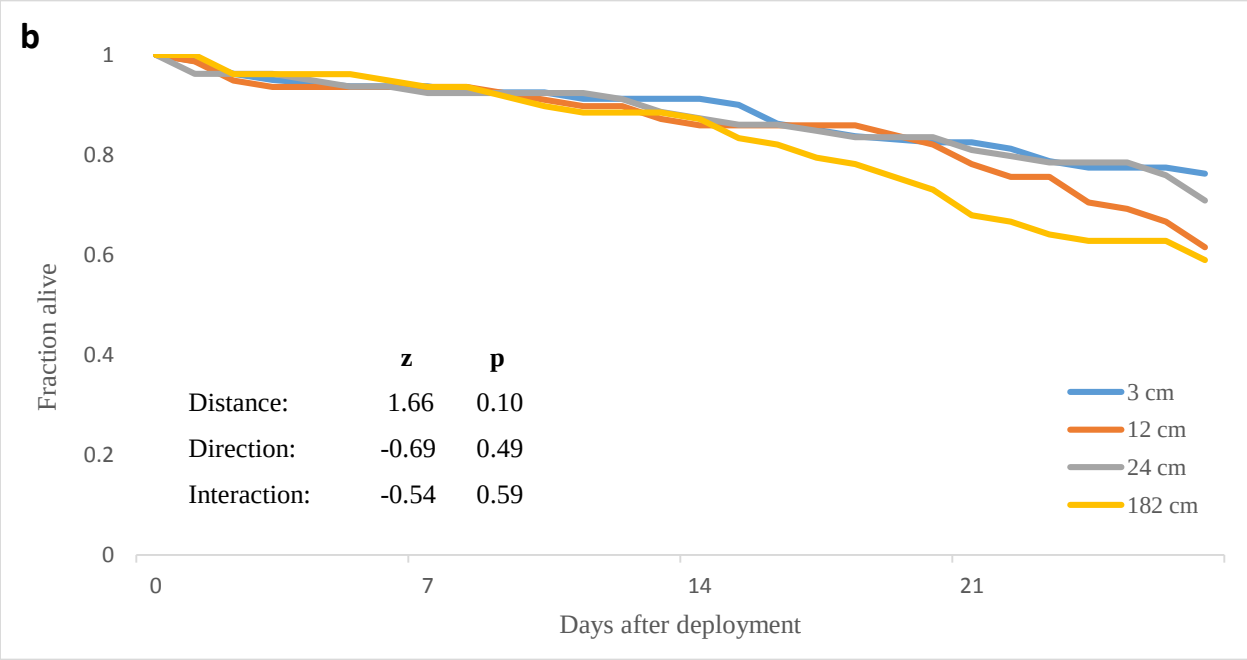


Figure 1- Survivorship for a) *Pocillopora damicornis* and b) *Seriatopora hystrix*

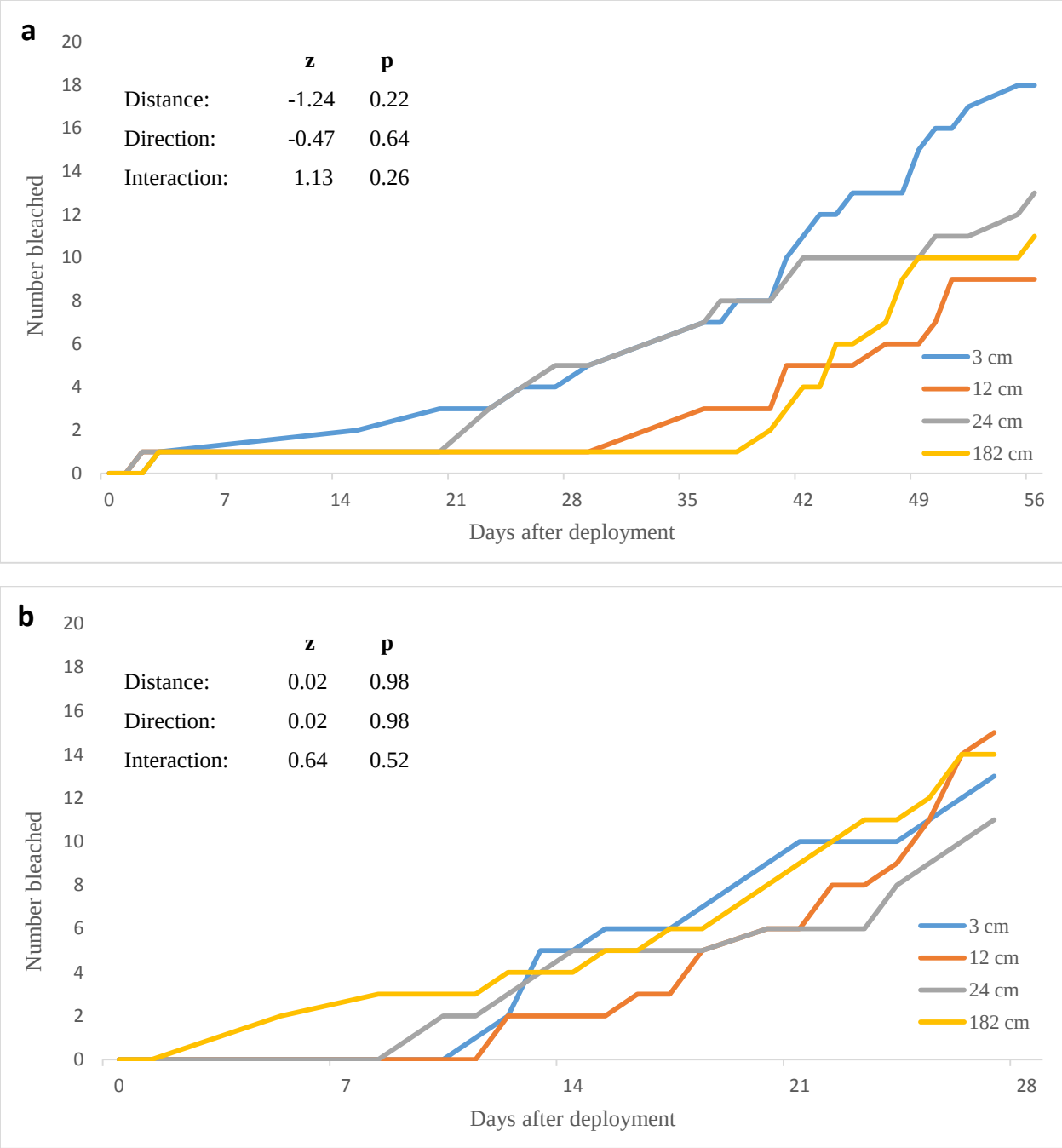


Figure 2- Cumulative number of fragments that bleached for a) *Pocillopora damicornis* and b) *Seriatopora hystrix*

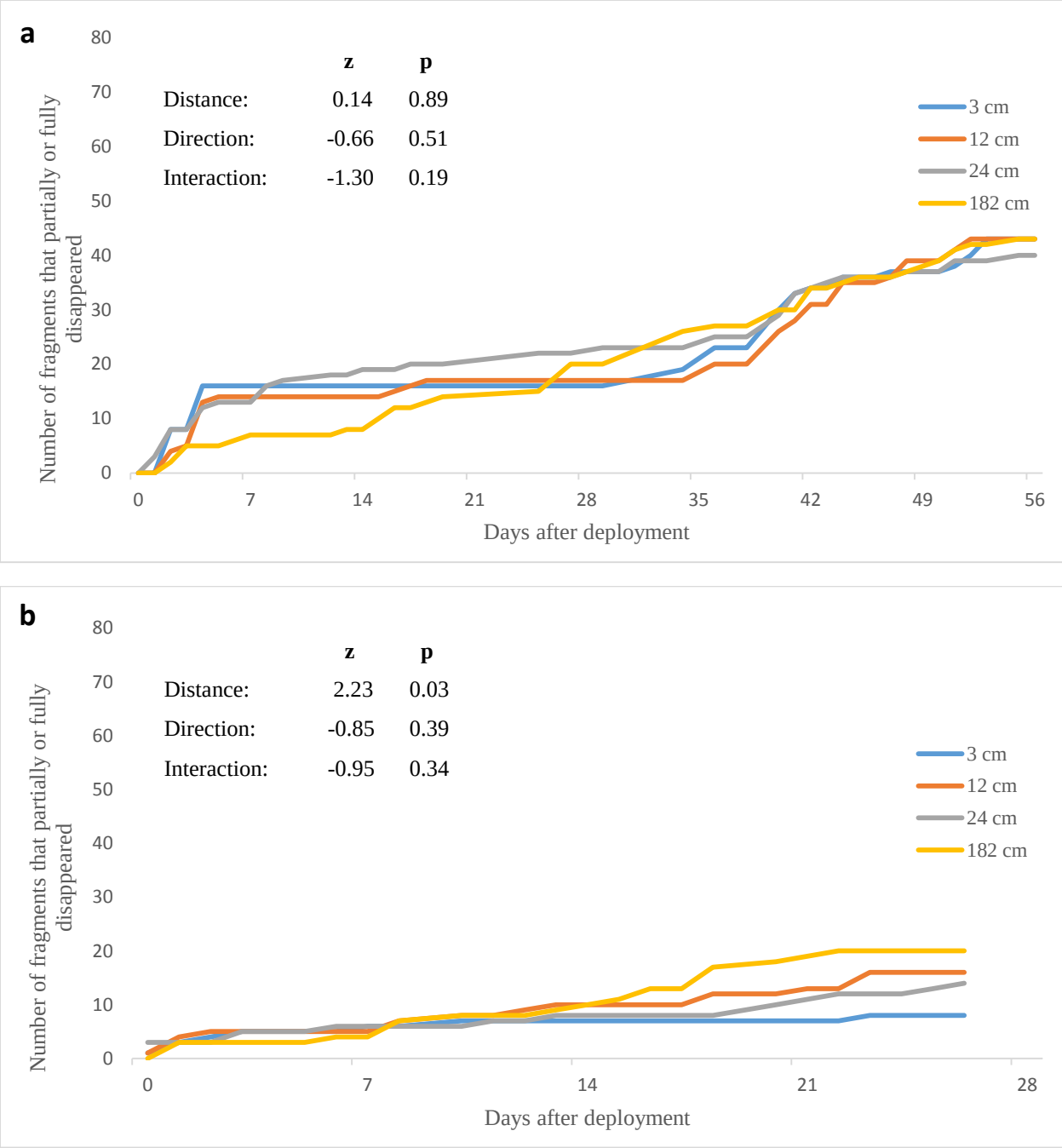


Figure 3- Cumulative number of fragments eaten for a*) Pocillopora damicornis* and b) *Seriatopora hystrix*

I further divided death due to putative predation between isolated predation incidents (death of one or two fragments on a tile in 24 h) and localized predation episodes (disappearance of three or four fragments from a tile in 24 h). I distinguished between these two types of putative predation because their causes were potentially different and therefore either one could have been distance-dependent or masked distance-dependence in the other. Six of 10 *P. damicornis* replicates experienced localized predation on at least one of their eight tiles; three of those experienced localized predation on three or more tiles within 24 h. Two of 10 *S. hystrix* replicates experienced localized predation (on one tile each). Because of the low number of localized predation episodes for *S. hystrix*, I further investigated localized predation only for *P. damicornis*.

The rapid and localized disappearance of numerous *P. damicornis* fragments in some replicates suggested spatially localized predation. To evaluate this, I removed tiles whose four fragments appeared eaten from around three focal colonies, replaced them with spare tiles holding healthy fragments (the "replacement tiles") and videotaped these tiles during the following high tides. All three sets of replacement tiles again experienced localized predation and their survival curve was significantly different from that of the replicates that had not experienced localized predation in the initial run (mixed effect Cox proportional hazards, $z=3.5$, $p<0.0005$) (Figure 4). Around two of these three focal colonies, the territorial triggerfish *Balistapus undulatus* was videotaped eating multiple fragments from multiple tiles. Thus, localized predation of *P. damicornis* appeared due to feeding by *B. undulatus.* In one case, I also noted a crown-of-thorns sea star (*Acanthaster planci*) eating both fragments and the focal *P. damicornis* over two days. I cannot unambiguously attribute all other instances of localized predation to *B. undulatus* but the events captured on video resulted in fragments irregularly

broken at or above the top of the epoxy, as was also seen for most localized predation episodes in the initial outplanting.

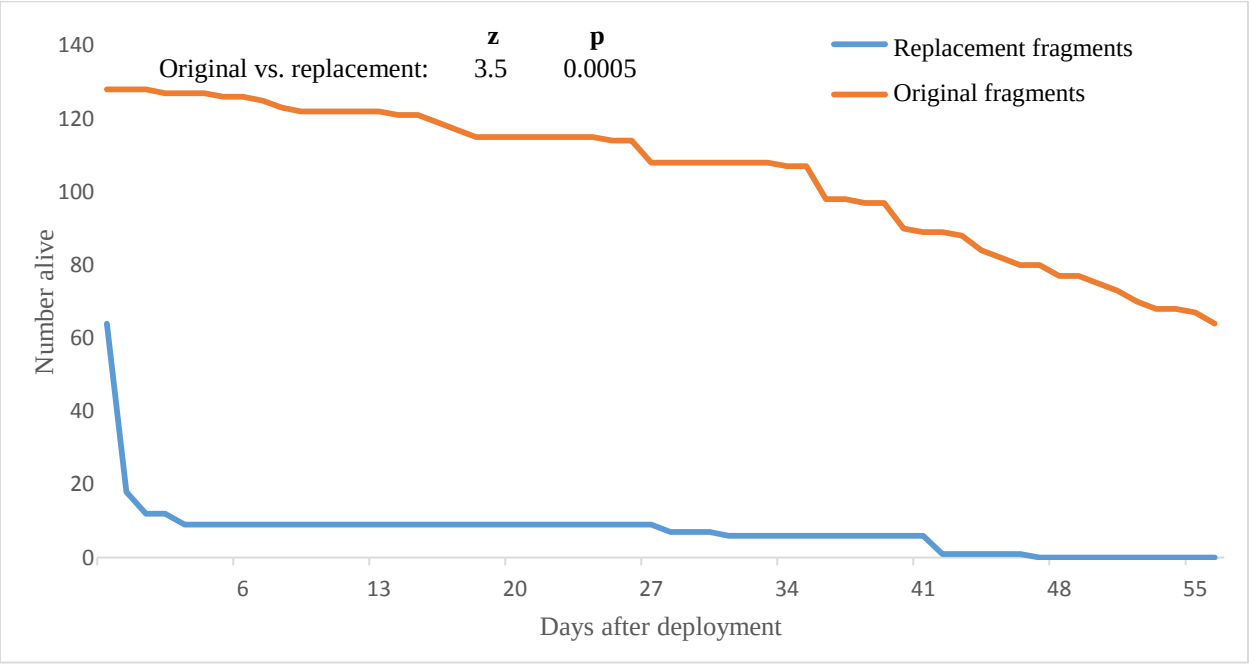


Figure 4- Survival of *Pocillopora damicornis* fragments around the four focal colonies that did not experience localized predation (original fragments) versus replacement fragments

Having established that localized predation occurred around some focal *P. damicornis* colonies, I examined whether localized predation was distance-dependent and whether it masked distance-dependent mortality in replicates which did not have localized predation. Distance did not significantly affect mortality in replicates that did not experience localized predation but direction nearly did (z=-1.88, p=0.06), with a trend for greater mortality downstream (west) of focal colonies (Figure 5a). Considering only replicates which experienced localized predation

(both original and replacement tiles), neither distance nor direction significantly affected mortality from all causes (Figure 5b) or just from localized predation (Figure 5c).

Pocillopora damicornis fragments were significantly more likely to die of putative predation as opposed to bleaching and dying in place than were *S. hystrix* fragments (chi-square test, χ^2=17.2, df=1, p<0.0001). More than three times as many *P. damicornis* fragments died from putative predation as bleached prior to death (169 vs. 47 out of 320, respectively), while only a few more *S. hystrix* fragments died from putative predation than bleached prior to death (58 vs. 46 out of 320, respectively). If replicates with localized predation were excluded, *P. damicornis* and *S. hystrix* appeared equally susceptible to other causes of mortality (primarily isolated predation incidents and bleaching) (χ^2=0.022, df=1, p=0.88).

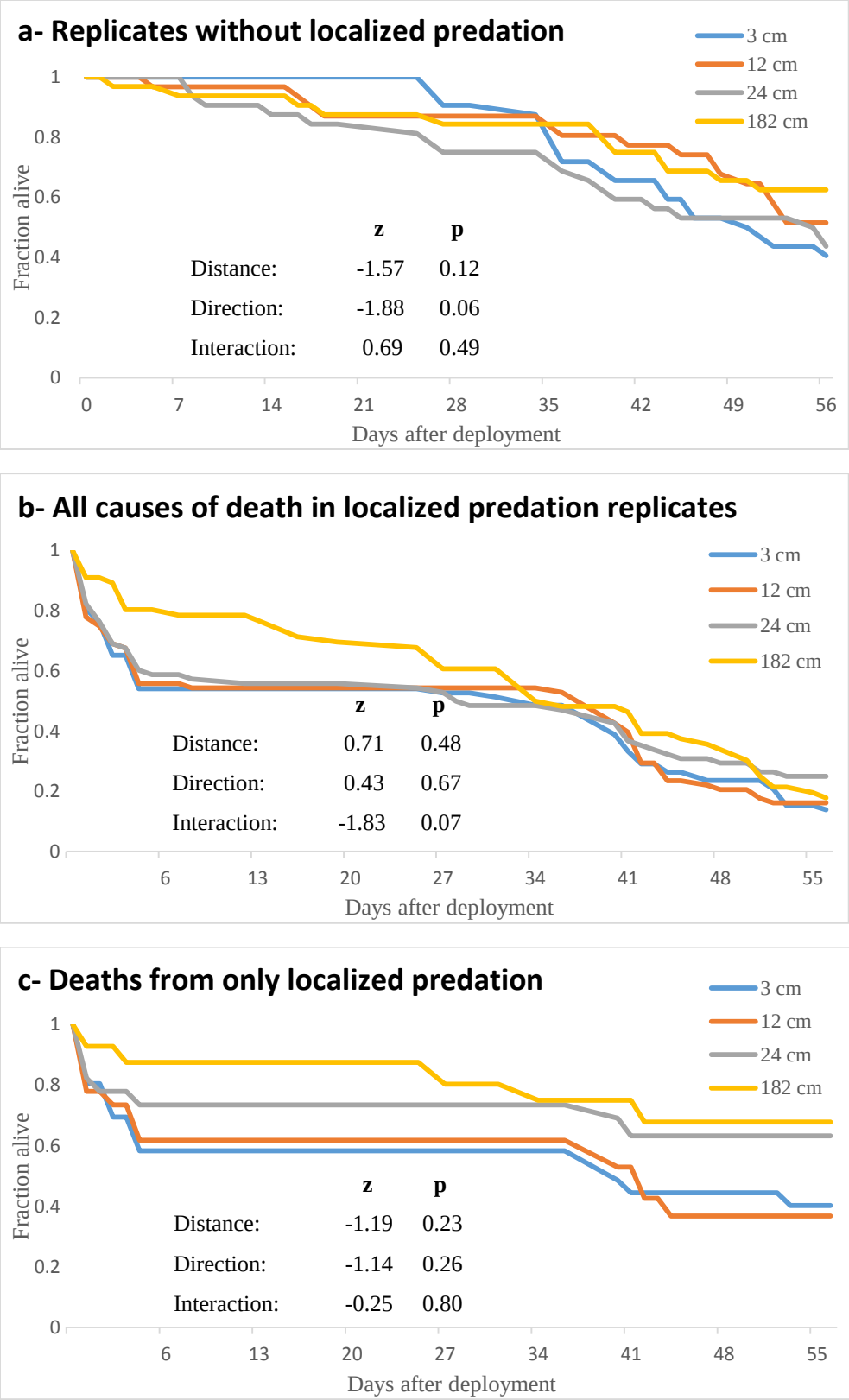


Figure 5- Survival with and without localized predation.

3.2 Distribution surveys

I analyzed spatial patterns using both entire 8 x 8 m plots and excluding habitat within these plots that was deemed unsuitable for *P. damicornis* or *S. hystrix* (e.g. sand-scoured channels and pools, bommie tops covered in dead coral rubble). Generally, the analyses using only suitable habitat were quantitatively similar to those using the entire plots but were more conservative. When unsuitable habitats were excluded, neighborhood density analysis indicated that both *P. damicornis* and *S. hystrix* were significantly aggregated at up to 1 m when all size classes were considered and surveys from all villages were pooled (Figure 6a & b). When analyzed by site, the distance below which colonies were aggregated ranged from < 1 m in Votua and Vatuo-lailai to nearly 3 m in Namada (Figures 9-20). At no distance on any reef were colonies significantly overdispersed.

I performed identical analyses with *P. damicornis* in size categories of <5 cm, $\geq$5 cm, $\geq$10 cm, and $\geq$15 cm diameter (Figure 6c-f). The largest colonies ($\geq$15 cm) were not aggregated at any scale, but all smaller size classes were strongly aggregated at scales of up to 1 m. Thus, the smaller colonies appeared to drive the aggregation at up to ≈1 m when I analyzed all sizes together, however, the sample size for large colonies was limited (n=187 colonies $\geq$15 cm across all three reefs), so that may constrain my ability to detect spatial patterns for large colonies.

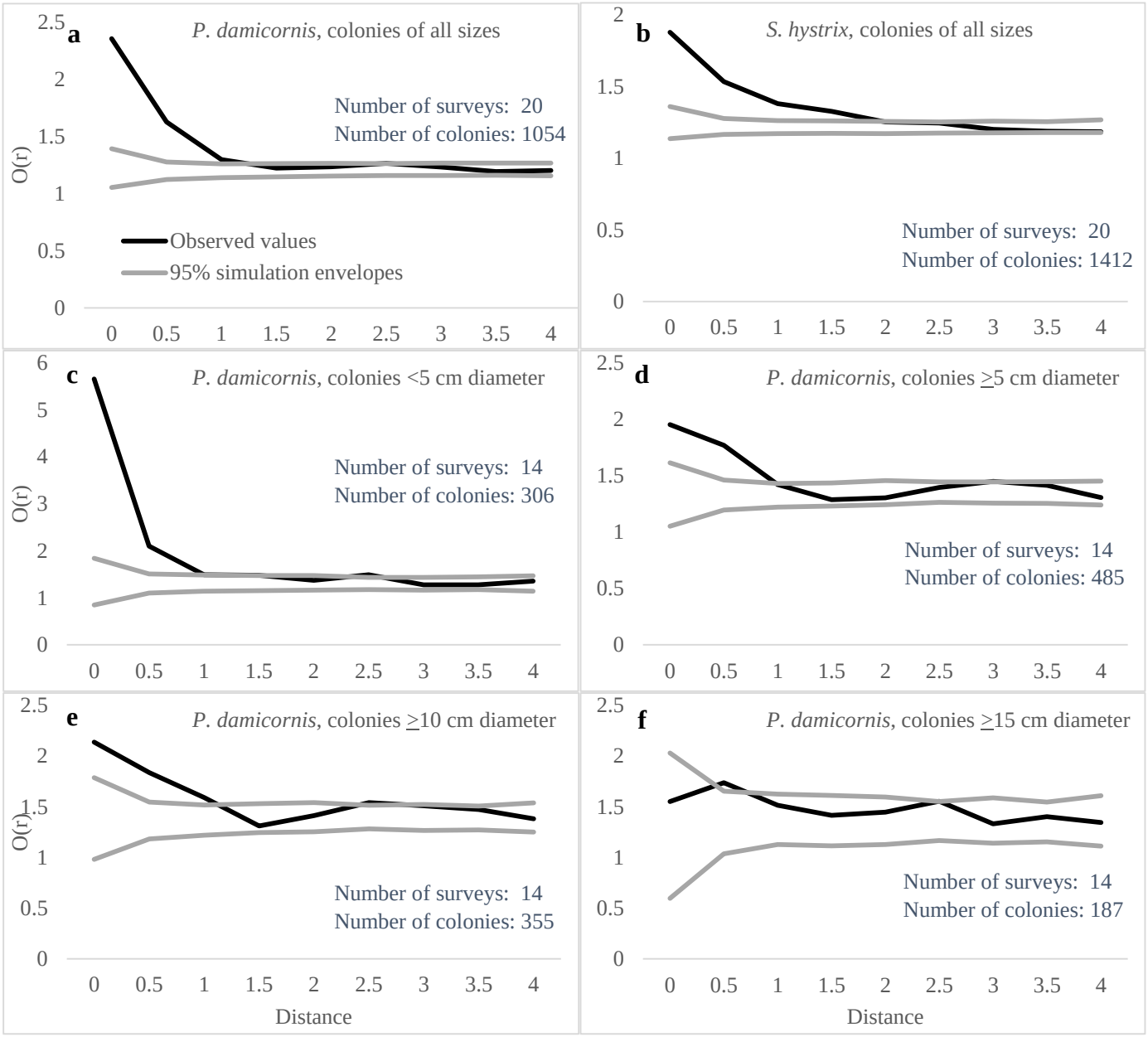


Figure 6- Neighborhood density analysis of *Pocillopora damicornis* and *Seriatopora hystrix* in 8 x 8 m quadrats with replicates from all three reefs combined

To resolve the spatial distribution of *P. damicornis* and *S. hystrix* more finely, I conducted separate circular surveys (radius = 2 m) around focal colonies that met specific criteria. Across all 2 m, there was a significant negative relationship between distance from focal *P. damicornis* colonies and *P. damicornis* count (corrected for area surveyed at each distance and henceforth called density), focal *P. damicornis* and radial *S. hystrix* density, and focal *S. hystrix* and radial *P. damicornis* density (GLM: $z=-4.4$, $p<0.0001$; $z=-3.9$, $p<0.0005$; $z=-3.6$, $p<0.0005$, respectively) (Figure 7). The relationships within the first 0.5 m or 1 m for these focal-radial combinations were not significant (see Table 1 for all values not provided in text).

Across all 2 m, there was no significant relationship between distance from focal *S. hystrix* colony and radial *S. hystrix* density (GLM, $z=-1.9$, $p=0.06$) (Figure 7b). However, there was a significant positive relationship between distance and density within the first 0.5 m (GLM, $z=-12.99$, $p<0.05$) but not within the first 1 m.

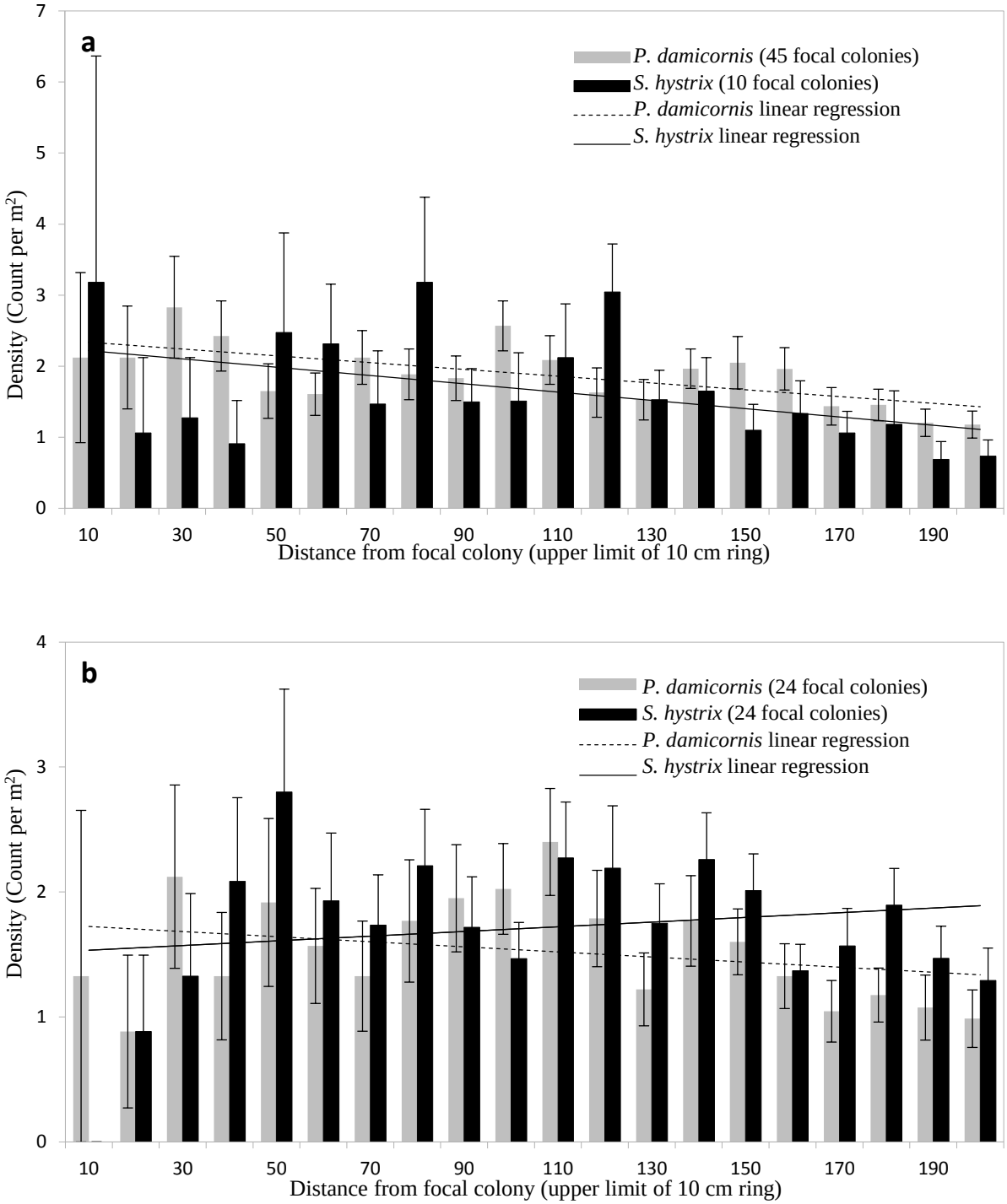


Figure 7- Density (+ SE) of *Pocillopora damicornis* and *Seriatopora hystrix* within 2 m of focal a) *P. damicornis* and b) *S. hystrix* colonies

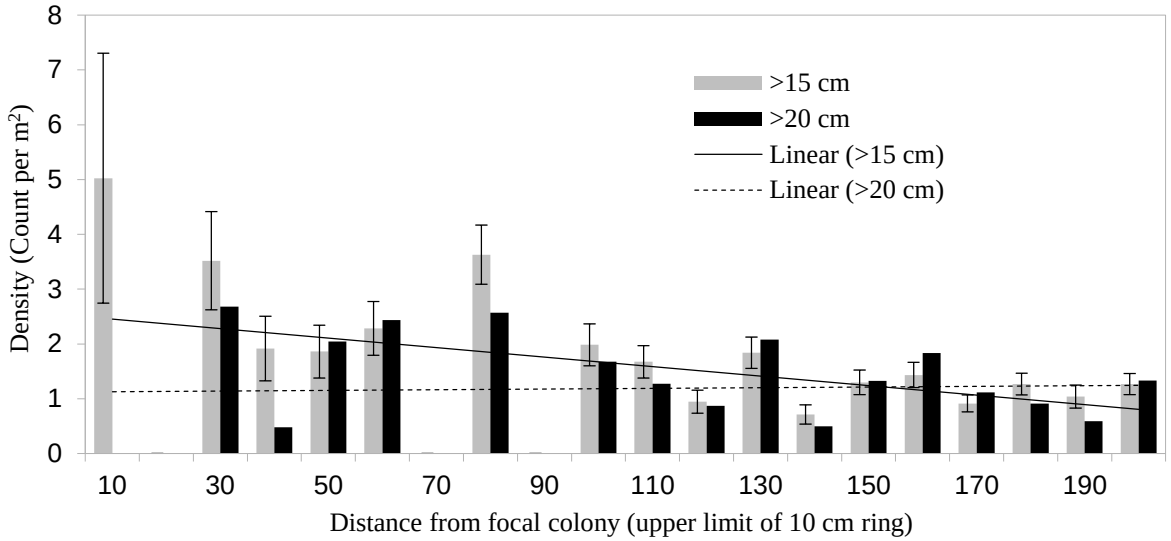


Figure 8- Density (mean + SE) of *Pocillopora damicornis* within 2 m of focal *P. damicornis* based on the 8 x 8 m surveys

Table 1- Colony counts within 2 meters of focal colonies

Focal species-radial species	Maximum distance	Slope	z value	p-value
P. damicornis-*P. damicornis*	0.50 m	-0.0098	-1.0	0.32
	1.0 m	0.00055	0.22	0.83
	2.0 m	-0.0032	-4.4	<0.0001
P. damicornis-*S. hystrix*	0.50 m	0.016	0.59	0.56
	1.0 m	0.0012	0.19	0.85
	2.0 m	-0.0057	-3.9	<0.0005
S. hystrix-*P. damicornis*	0.50 m	0.0099	0.57	0.57
	1.0 m	0.0042	1.1	0.28
	2.0 m	-0.0036	-3.6	<0.0005
S. hystrix-*S. hystrix*	0.50 m	0.042	2.3	<0.05
	1.0 m	-0.00065	-0.18	0.86
	2.0 m	-0.0017	-1.9	0.06

I converted the 8 x 8 m surveys into data analogous to the circular surveys for comparison. Considering any *P. damicornis* colony ≥15 cm across as a focal colony and any smaller individual as a radial colony, there was a significant negative relationship between distance and radial *P. damicornis* density (GLM, $z=-3.6$, $p<0.0005$) across all 2 m but not across the first 0.5 m or 1 m (Figure 8; Table 2). However, when the cutoff for focal colonies was 20 cm, there was no relationship between distance and *P. damicornis* colony count at 0.5 m, 1 m, or 2 m (Figure 8; Table 2).

Table 2- Colony counts from 8 x 8 m surveys within 2 m of focal colonies

Threshold size for focal colony	Maximum distance	Slope	z value	p-value
15 cm	0.50 m	-0.0064	-0.46	0.65
	1.0 m	-0.0063	-1.5	0.14
	2.0 m	-0.0034	-3.6	<0.0005
20 cm	0.50 m	0.047	1.2	0.23
	1.0 m	0.00032	0.045	0.96
	2.0 m	-0.0016	-1.09	0.27

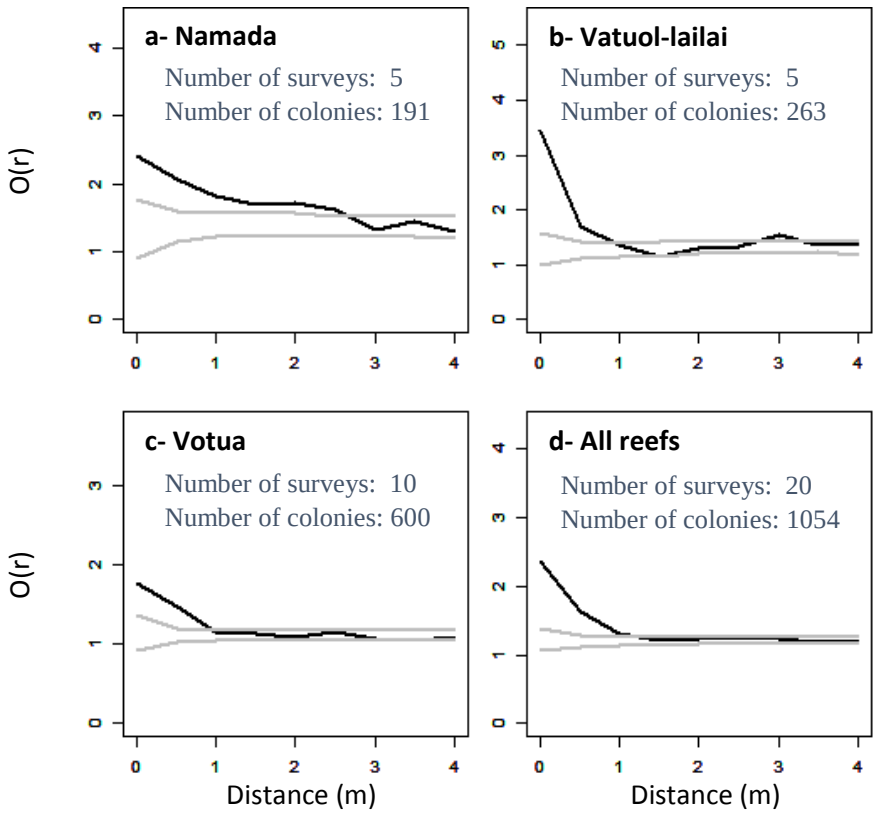


Figure 9- *P. damicornis* of all sizes using only suitable substrate

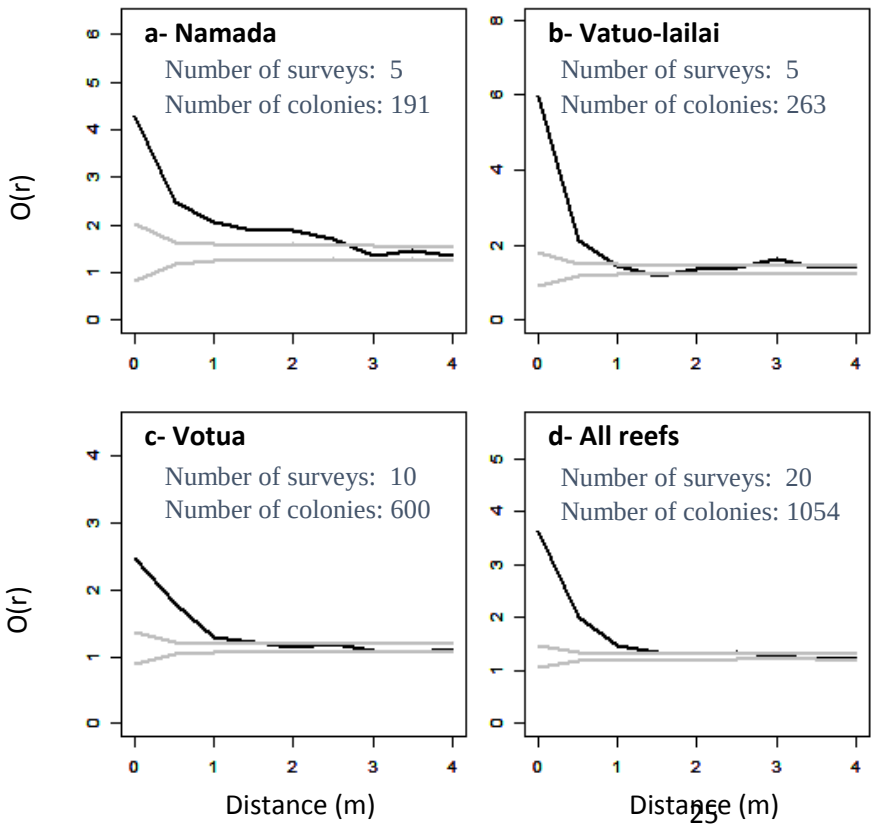


Figure 10- *P. damicornis* of all sizes using all 8 x 8 m

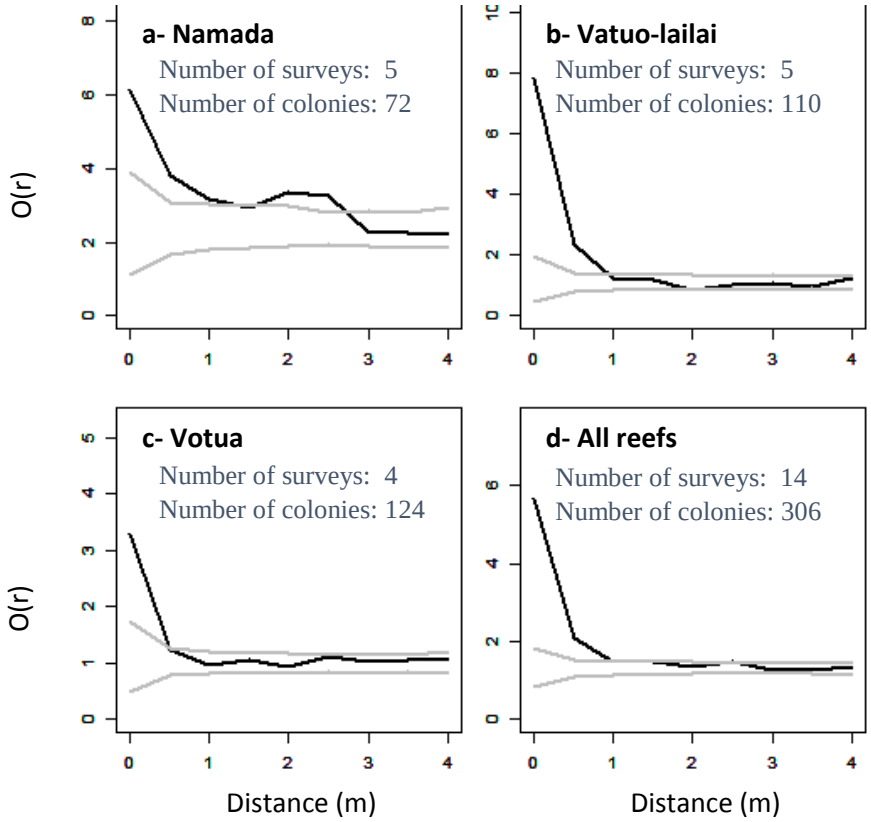


Figure 12- *P. damicornis* <5 cm using only suitable substrate

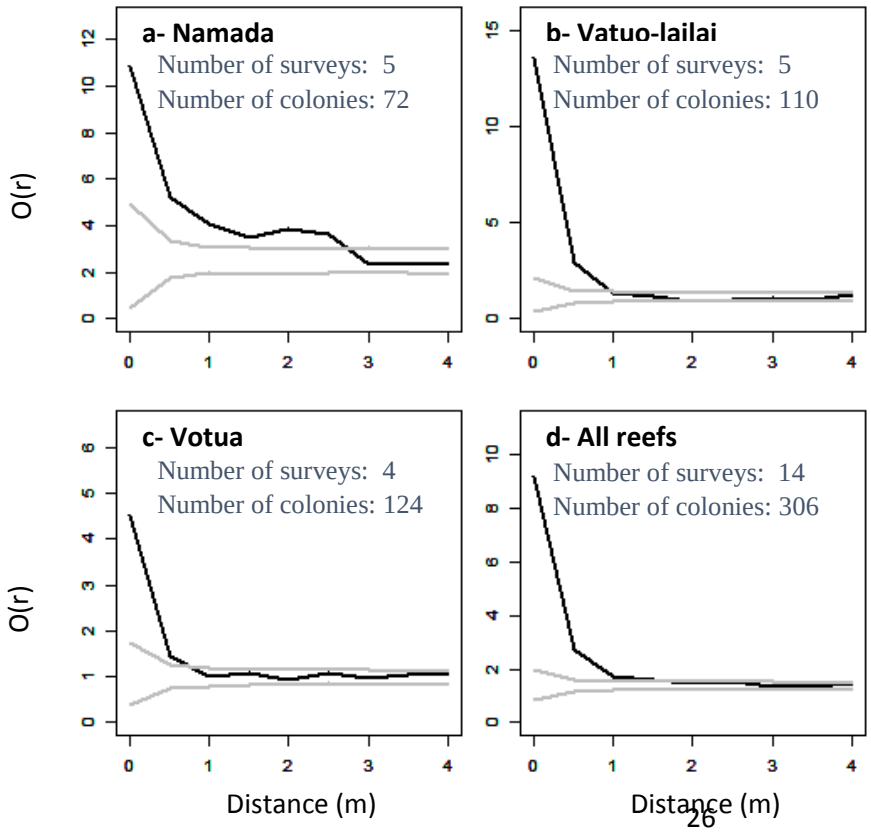


Figure 11- *P. damicornis* <5 cm using all 8 x 8 m

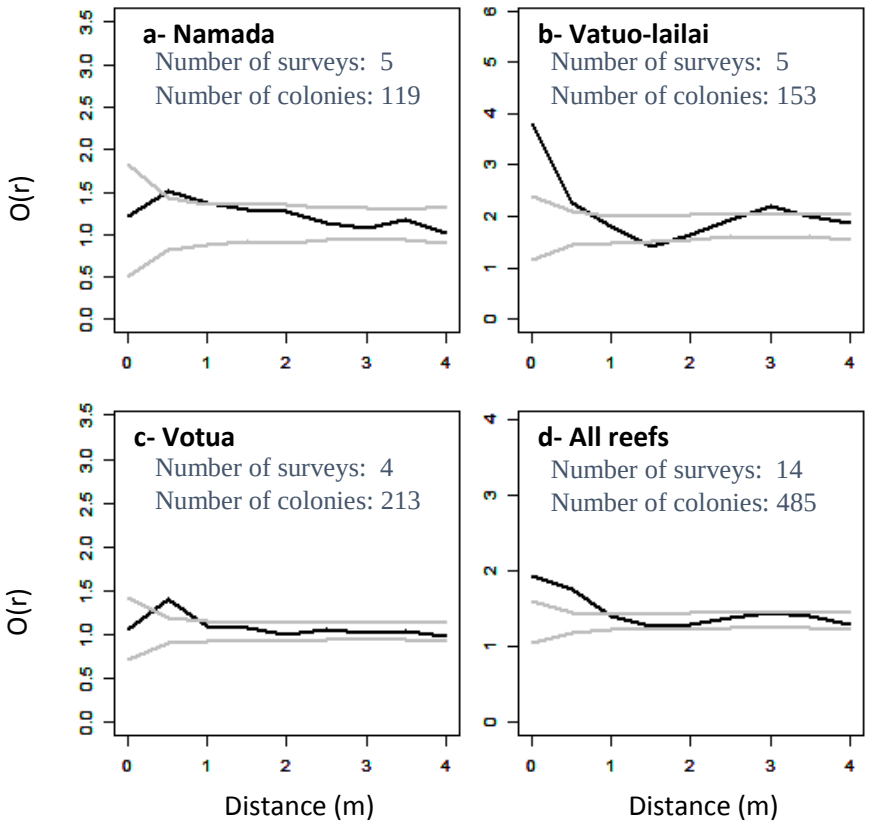


Figure 13- *P. damicornis* ≥5 cm using only suitable substrate

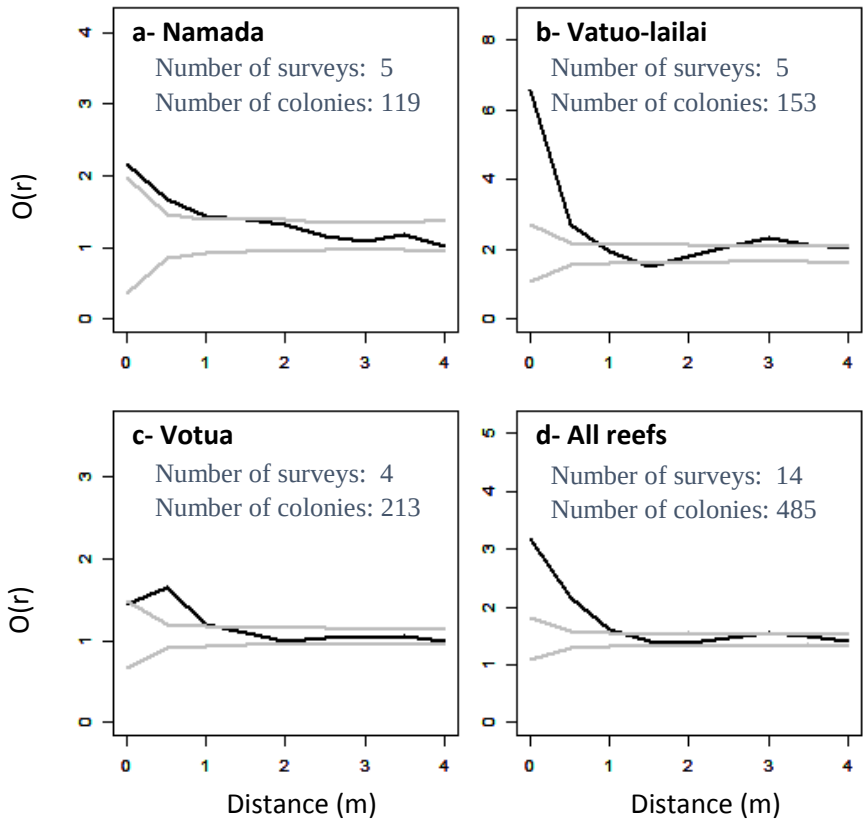


Figure 14- *P. damicornis* ≥5 cm using all 8 x 8 m

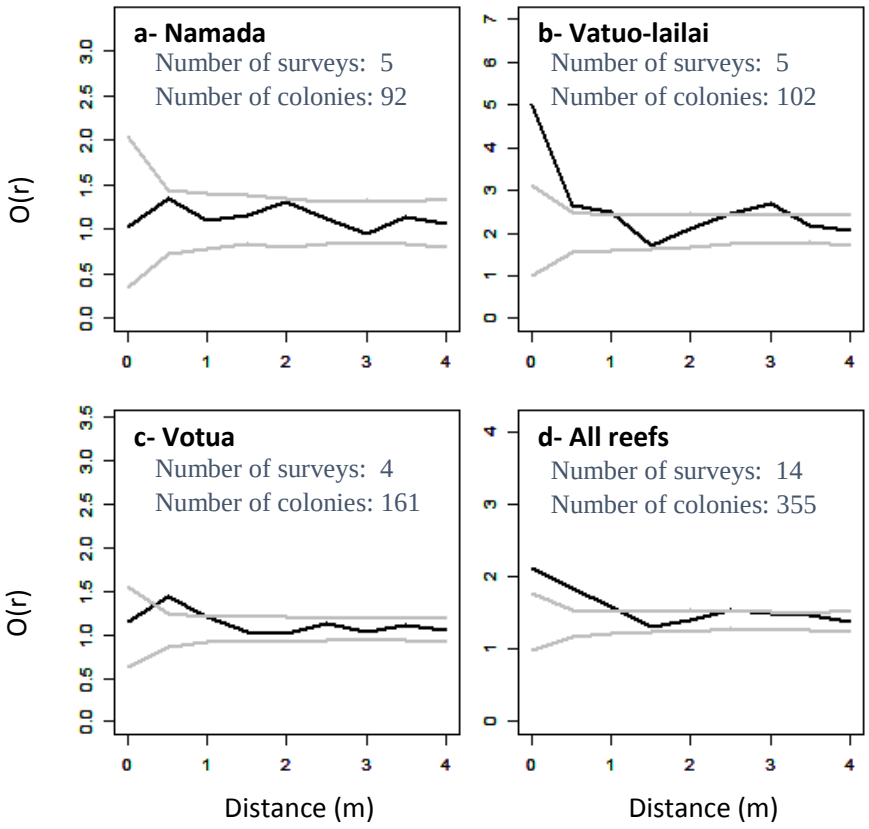


Figure 15 - *P. damicornis* ≥10 cm using only suitable substrate

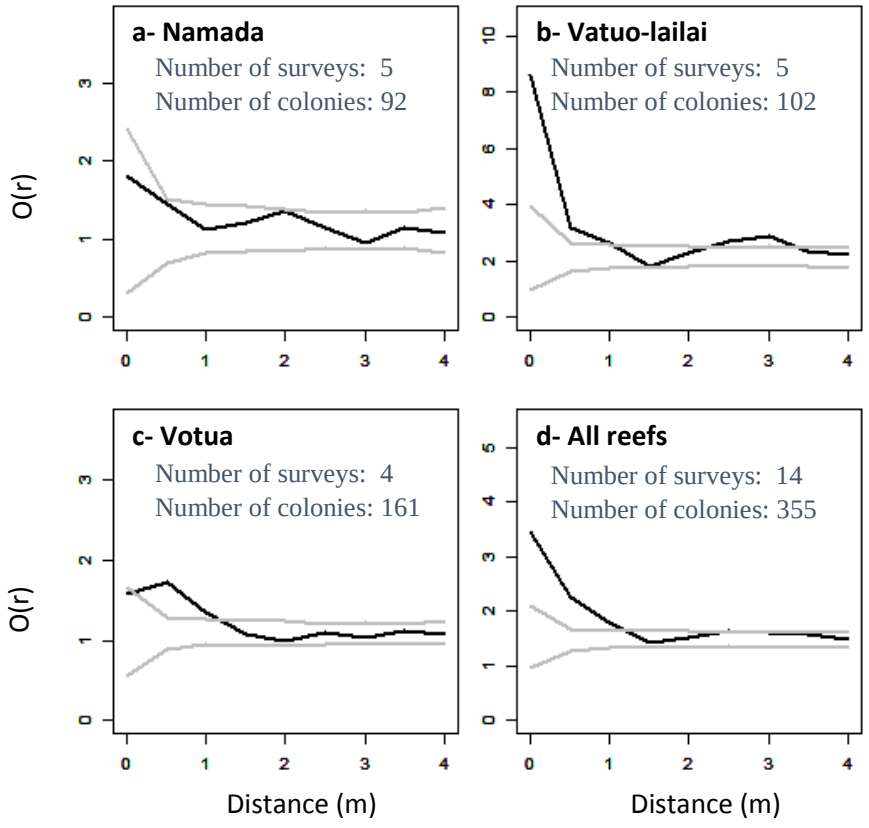


Figure 16- *P. damicornis* ≥10 cm using all 8 x 8 m

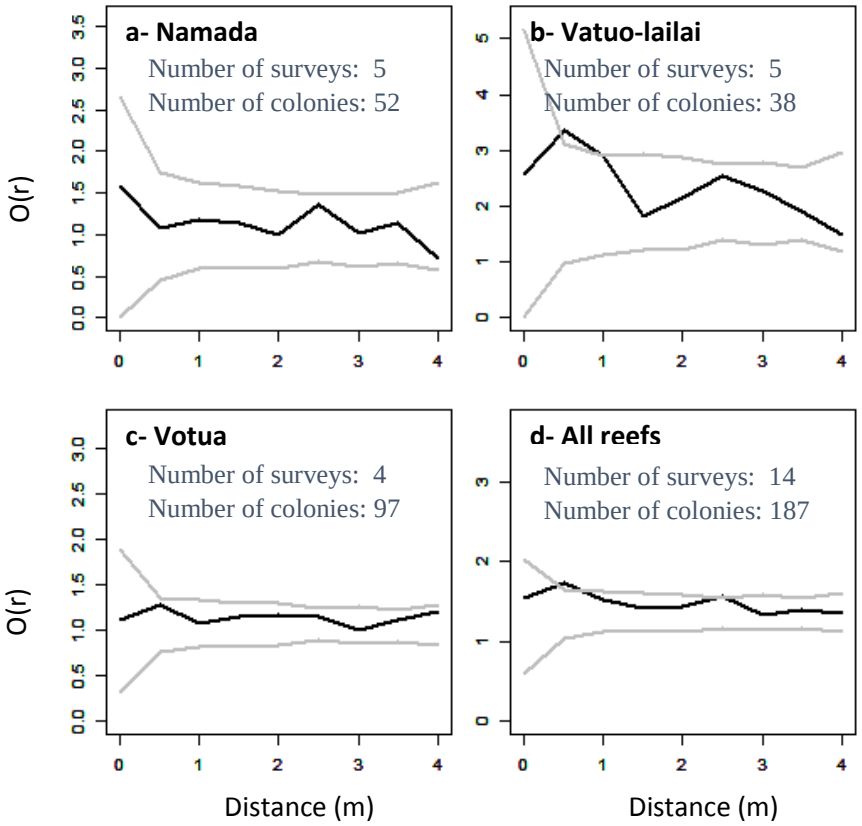


Figure 17- *P. damicornis* ≥15 cm using only suitable substrate

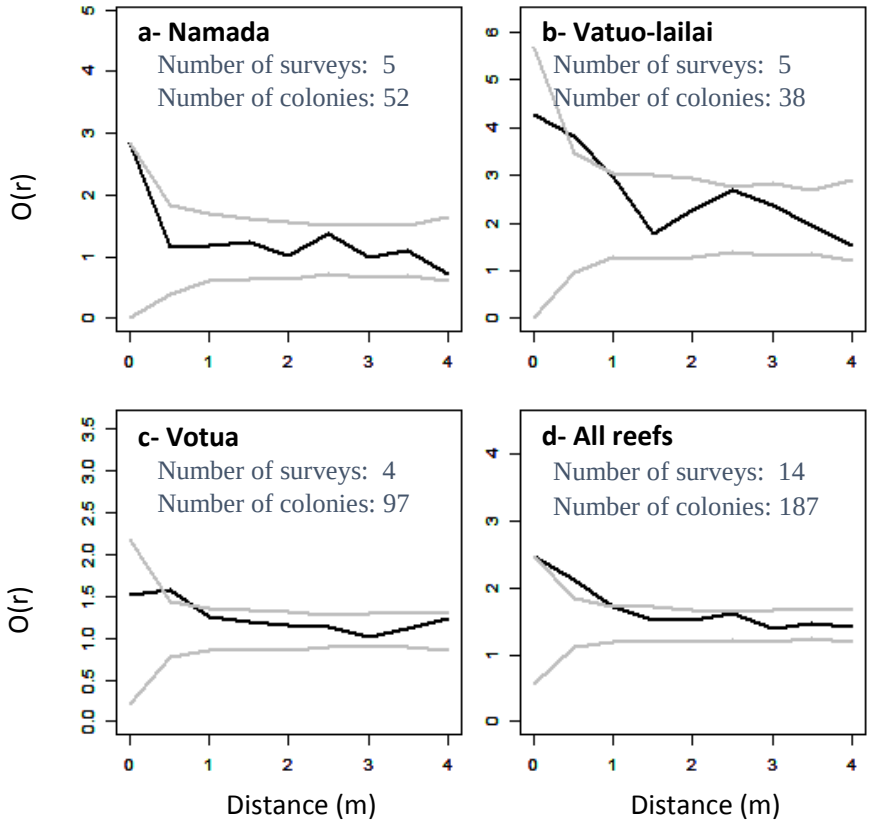


Figure 18- *P. damicornis* ≥15 cm using all 8 x 8 m

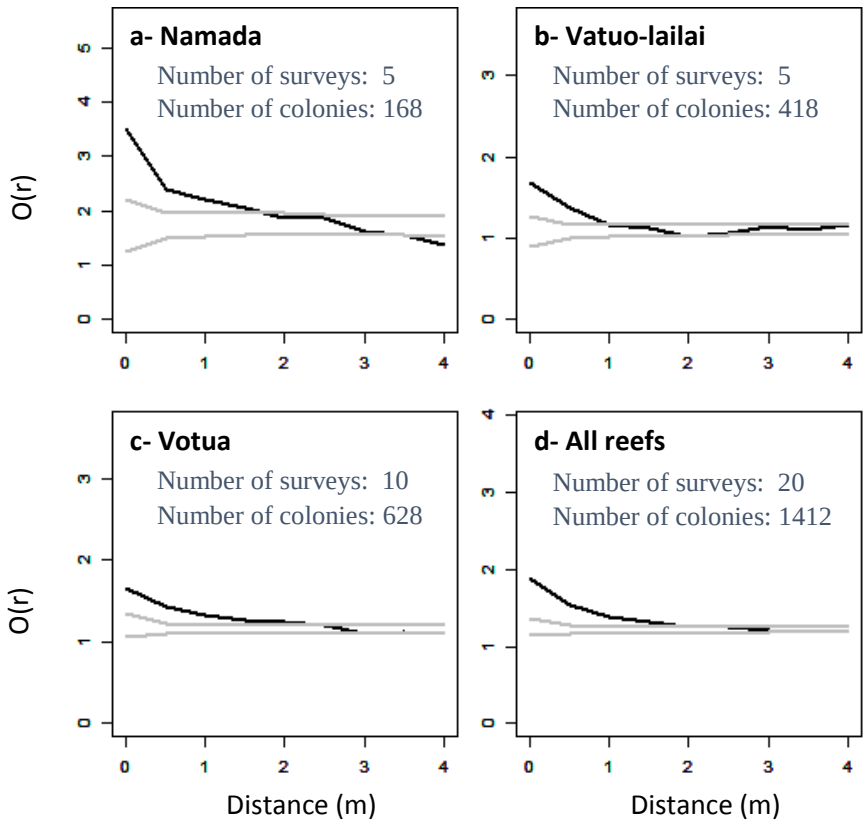


Figure 19- *S. hystrix* of all sizes using only suitable substrate

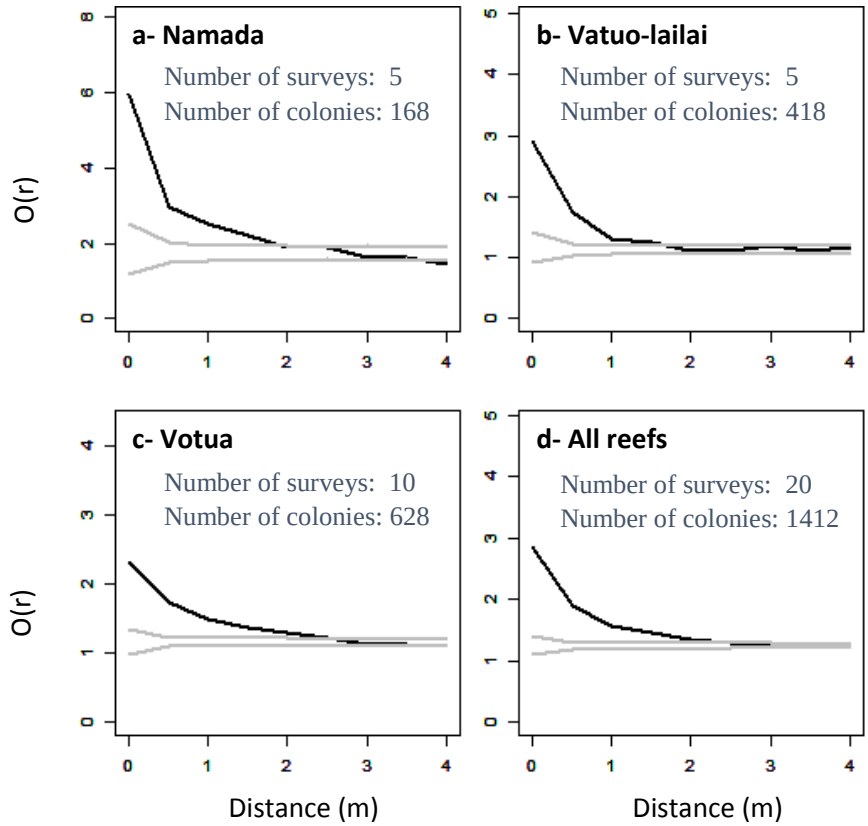


Figure 20- *S. hystrix* of all sizes using all 8 x 8 m

CHAPTER 4: DISCUSSION

I tested multiple predictions of the Janzen-Connell hypothesis using two abundant coral species that are confamilial brooders. Survival experiments with *P. damicornis* and *S. hystrix* fragments did not support distance-dependent mortality of juvenile-sized colonies around conspecific adults as posited in the Janzen-Connell hypothesis (Figure 1). The only evidence for distance-dependent mortality was for putative predation of *S. hystrix,* where mortality increased rather than decreased with distance from adult colonies (Figure 3b). This would produce the observed aggregation (Figure 6) rather than overdispersion, in opposition to the Janzen-Connell hypothesis. The general lack of distance-dependent mortality in this study is consistent with a meta-analysis of distance-dependent mortality studies of the seeds and seedlings of terrestrial plants (Hyatt et al. 2003), in which distance from parents did not affect overall survival. However, when separated by life stage, seedling survival increased with distance from parents while seed survival was not affected, suggesting that distance-dependent mortality may only emerge at certain life stages. This motivated my use of coral fragments that are approximately the size of 6 month old recruits (Sato 1984). It is important to note, however, that if distance-dependent mortality acts only on younger stages of these species (e.g., newly settled larvae), the transplants would not have detected this effect.

The importance of Janzen-Connell effects can also be evaluated by characterizing the spatial arrangement of conspecific colonies on the reef, with overdispersion predicted (Janzen 1970; Connell 1971). These spatial analyses might uncover patterns, whether aggregation or overdispersion, generated by mortality among new settlers that my experiment would not detect. The observed spatial pattern represents the balance of multiple, potentially opposing forces –

such as high density of recruits near brooding parents (similar to terrestrial seed shadows) vs possible detrimental effects of adult-associated enemies on nearby recruits (Marhaver et al. 2013). Contrary to the predictions of the Janzen-Connell hypothesis, I found significant clumping within about 1 m or less of conspecifics, rather than overdispersion, for both *P. damicornis* and *S. hystrix* (Figure 6a & b). The 8 x 8 m surveys and the 2 m radius surveys both supported this pattern; there was a significant negative relationship between *P. damicornis* radial colony density and distance from focal *P. damicornis* and a nearly significant negative relationship (with a much more limited sample size) between *S. hystrix* radial colony density and distance from focal *S. hystrix* (Figure 7). However, I also observed a significant negative relationship between *S. hystrix* density and distance from *P. damicornis* and *P. damicornis* density and distance from *S. hystrix* (Figure 7), suggesting that the cause of declining density was not species-specific. Given that *P. damicornis* and *S. hystrix* are confamilial, an enemy that prefers one coral species in this family might generate this pattern among multiple confamilial species (e.g. butterflyfish that prey upon multiple *Acropora* species [Pratchett 2007]).

Both the survival experiment and survey evidence suggested that distance-dependent mortality was not generating a minimum distance between conspecific colonies of either species, as predicted by the Janzen-Connell hypothesis. Rather, they are consistent with the invariant survival model of the relationship between distance and establishment (Nathan and Casagrandi 2004), in which recruitment declines with distance from parents and survival is constant with distance from parents. This produces declining establishment of offspring with distance from parents. Invariant establishment is one of five possible outcomes from the interaction of recruitment and survival curves, the best known of which is the Janzen-Connell relationship.

There are many potential causes for the observed clumping of conspecifics that do not assume invariant survival with distance. These include: more favorable substrates for *P. damicornis* and *S. hystrix* closer to focal colonies, gregarious settlement, larger colonies producing safe-sites for smaller ones, and short dispersal distances (Carlon and Olson 1993), perhaps to improve fertilization success of brooding corals under sperm limitation (Brazeau and Lasker 1992, Grosberg 1987 for an example with a colonial, brooding ascidian, and Phillippi et al. 2004 for a counterexample).

The potential for aggregated settlement near adults may be considerable because *P. damicornis* and *S. hystrix* are brooding species producing planular larvae that can settle quickly after release (Atoda 1951; Richmond 1987; Isomura and Nishihira 2001). Some studies of pocilloporid dispersal note a tendency for planulae to settle near their parents (Underwood et al. 2007; Torda et al. 2013), and even if planulae disperse several meters, they may still preferentially settle near conspecific adults (Babcock 1998; Tioho et al. 2001). Moreover, pocilloporid recruitment is spatially heterogeneous (Dunstan and Johnson 1998) and occurs in hotspots that may be partially determined by water flow and density of adult confamilials (Eagle 2006). Additionally, *P. damicornis* planulae preferentially settle on the encrusting coralline alga *Titanoderma prototypum* (Price 2010); this could generate aggregations if *T. prototypum* is patchily distributed. Any, or all, of these processes could aggregate early life stages of *P. damicornis* and *S. hystrix*.

Post-settlement processes may also contribute to the aggregation. Corals experience high mortality within several weeks of settling (Glassom and Chadwick 2006) and their community composition and spatial distribution may change in that time (Penin et al. 2010). Changing spatial distribution over time appeared to occur at these sites as evidenced by *P. damicornis* <5

cm in diameter being clumped at a scale of <1 m, while the largest colonies (≥15 cm) were not clumped at any distance assessed. This accords with weaker aggregation among adult trees in a subtropical forest than among saplings or juveniles, attributed to self-thinning at the juvenile-adult boundary rather than to species-specific enemies (Zhu et al. 2013). Alternatively, the absence of aggregation among larger *P. damicornis* colonies may be due to a lack of statistical power. There were many fewer large colonies, and this would limit my ability to rigorously detect distribution patterns.

The only other direct test of the Janzen-Connell hypothesis in corals was conducted on the planulae and recruits of broadcasting *Orbicella* (formerly *Montastrea*) *faveolata* in the Caribbean (Marhaver et al. 2013). In that study distance-dependent mortality was inferred to be microbially mediated, with effects differing upstream and downstream of focal *O. faveolata*. However, the results of that study and my study are not directly comparable.

First, Marhaver et al. (2013) used planulae and recruits a few days old in their distance-dependent survival experiments, whereas I used fragments taken from mature colonies; the processes structuring their mortality may differ (Harriott 1983; Christiansen et al. 2009). For example, in the present study only about one quarter of *P. damicornis* fragments that died bleached beforehand, and liberally assuming that microbes caused every bleaching means that microbes still only caused one quarter of *P. damicornis* deaths. For *S. hystrix*, putative predation and bleaching were involved in roughly equal numbers of deaths. In contrast, Marhaver et al. assumed that all mortality of new recruits was microbe-related. Yet even examining only fragments that bleached in my study, I found no evidence of distance-dependent mortality for either species (Figure 2).

Second, *P. damicornis* and *S. hystrix* reproduce by brooding, with planulae able to settle soon after release (Atoda 1951; Richmond 1987; Isomura and Nishihira 2001); a relatively high proportion of planulae from these species likely settle within a few meters of their parent colony compared to broadcast spawners, whose gametes may disperse further on average (Tioho et al. 2001; Underwood et al. 2007). In this way, brooder dispersal is more akin to wind-driven seed dispersal among trees than is broadcast spawning. Indeed, Dunstan and Johnson (1998) found that the magnitude of spatial variation in brooder recruitment was greater than that of broadcasting corals across multiple years on the Great Barrier Reef. If there is greater spatial variation in brooder recruitment than broadcaster recruitment at my study site, then species-specific enemies might have different opportunities to attack brooded and broadcast settlers post-recruitment. For example, one might expect species-specific enemies that cause distance-dependent mortality to be more prevalent among species whose offspring often settle within meters of their parents or conspecific adults. Yet I observed neither the process (distance-dependent mortality) nor the predicted overdispersion that would result from this process.

Additionally, I conducted my survival experiments in situ on a speciose coral reef, whereas Marhaver et al. (2013) conducted their field experiments by transplanting focal adult colonies and new recruits onto more simple, open sand flats. By using in situ focal colonies amidst a diverse assemblage of other species, my experiments may have been less sensitive but more ecologically realistic than those of Marhaver et al. (2013). Distance-dependent mortality of *P. damicornis* and/or *S. hystrix* could have occurred but been obscured on the reef studied here by other causes of mortality. For example, had I deployed fragments around focal colonies transplanted to sand channels (making the surrounding community much less diverse), I might

have avoided the territories of *B. undulatus* and the ensuing localized predation, in turn revealing, and possibly accentuating, other causes of mortality.

While I did not find support for distance-dependent mortality, I did observe spatially heterogeneous corallivory on *P. damicornis*, which may promote species coexistence by producing a mosaic of favorable and unfavorable patches across the reef (Levin and Paine 1974; Holt 1984). Corallivore activity is known to structure coral distribution on reefs in both the Pacific and Caribbean (Neudecker 1979; Littler et al. 1989) and parrotfish and butterflyfish density may impact recruit (1-10 mm) and juvenile (1-5 cm) coral mortality, respectively (Penin et al. 2010, see also Rotjan and Lewis (2008) for summary). Localized predation by the orange-lined triggerfish *B. undulatus* on small *P. damicornis* may have a similar effect here. *Balistapus undulatus* is a generalist with territories of 100-200 m^2 (McClanahan 2000) and eats the tips of branching corals, including *P. damicornis* (Hiatt and Strasburg 1960; Neudecker 1979). However, I did not observe *B. undulatus* consuming the tips of focal colonies in this experiment, suggesting that either territorial defense or a preference for small corals drove the pattern of predation on fragments. This triggerfish species' territoriality may delineate certain patches on reefs in which some species (e.g. *P. damicornis*) have high mortality while other species (e.g. *S. hystrix*) are not directly affected, akin to what is seen with seaweed in territories of the steephead parrotfish on the Great Barrier Reef (Welsh and Bellwood 2012) or *Pocillopora* and *Pavona* in the interaction between damselfish territories and roving corallivores in the Eastern Pacific (Wellington 1982). Additional experiments are necessary to determine how patchy corallivory contributes to the distribution and coexistence of *P. damicornis*, *S. hystrix*, and corals in general.

Additionally, I found that approximately 15% of the 640 small fragments I transplanted 5-15 cm above the benthos bleached, while none of the 128 fragments on the coral rack

bleached, despite being on the same reef and differing only by being located ≈1 m above the benthos. It is possible that when corals experience stress, those closer to the bottom are more exposed to enemies such as ciliates and flatworms that can live on other benthic species but also consume coral tissues and cause bleaching-like symptoms (Bender et al. 2012, Rawlinson and Stella 2012, Sweet et al. 2013, Hume et al. 2014), while corals raised above the bottom (like those on the coral racks) more easily avoid these little-noticed consumers.

In conclusion, I found no evidence for either the process of distance-dependent mortality or its resulting pattern in two brooding coral species on reef flats in Fiji. On the contrary, I found both *P. damicornis* and *S. hystrix* aggregated at the scale of about 1 m or less, with a tendency for small colonies to be clumped around larger ones. These findings are inconsistent with the Janzen-Connell hypothesis for diversity maintenance in species rich communities, suggesting that Janzen-Connell effects are not dominant on brooding corals on the species-rich reefs I investigated. Instead of distance-dependent mortality caused by species-specific enemies, I observed spatially heterogeneous corallivory on *P. damicornis*; this could facilitate species coexistence by delineating reef patches that are more or less favorable to certain coral species.

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